tribution and more or less evanescent in continuity, to the streams that flowed constantly in one direction and eventually into an unnatural habitat, the sea. They needed a more direct and quicker embryonic development, requiring, it would seem, the abandonment of the nauplius stage. It may therefore well be that the trilobites retaining the nauplius stage did not give rise to these stocks, as is sometimes assumed. We may have to look for this ancestral stock in one still more primitive, and the Protocaris-Apus line of branchiopods suggests itself, but whatever the stock, it would seem to have permanently invaded the rivers of the land either in Proterozoic time, or that postulated intermediate stage in the earth's history previous to the Cambrian but of which we have not a trace of direct evidence, the Lipalian time of Walcott.

[1] T. C. Chamberlin, *Jour. Geology*, 8, 400-412 (1900).
[2] J. Barrell, *Bull. Geol. Soc. America*, 27, 345-436 (1916).
[3] M. O'Connell, *Bull. Buffalo Soc. Nat. Hist.*, 11, No. 3, 1-277 (1916).
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OBSERVATIONS UPON TROPICAL FISHES AND INFERENCES FROM THEIR ADAPTIVE COLORATION

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Received by the Academy, November 24, 1916

The conception that species have been multiplied by divergent evolution of related strains is based upon a great body of verifiable observations. Sound judgment has not been exercised consistently, however, in the attempt to establish the fact that their development has been directed throughout by natural selection.

If the Darwinian hypothesis is true, the characters of organisms should be largely of an adaptive sort, but its adherents have failed, upon the whole, to distinguish between shadow and substance, and have been content to support their position by *imputing* utility to structures and habits, when nothing less than rigorous proof of the fact will suffice. It is not demonstrated, for example, that any class of markings serves for purposes of recognition, or for signalling between individuals of one species. Neither is it proved that some color combinations warn off possible enemies, nor, indeed, that any type of pigmentation is functionally conspicuous. The last assumption, nevertheless, underlies a series of suggestions whose apparent conformity with its terms is held to support the hypothesis of natural selection.

Under the auspices of the Tortugas Marine Laboratory of the Carnegie Institution of Washington, I have been enabled to study many of the bright-hued fishes of the West Indian region, and have attempted to place the facts regarding their coloration upon an objective basis.

Countershading appears almost universally upon these animals. That is to say, their pigments which are externally visible are definitely graded from darkest on the mid-dorsal, or upper, to lightest on the mid-ventral, or lower line. Exceptions to the rule occur only among species of unusual habit or peculiar form.

The systems of pigmentation indicated is no immediate effect of exposure to light, although it involves the production of dark shades in any region in direct proportion to the average intensity of the illumination of that part. This is shown clearly by certain cases of sexual dimorphism in the color of crabs. In the *Portunidae* the abdomen of the ovigerous female is exposed in dorsal view. In correlation with this family character the sexes differ in the coloration of that organ long before sexual maturity, when for the first time its position differs in the two. The abdomen of the male agrees in color with its sternum, but when that of the female is elevated it extends the pigment of the carapace posteriorly over the egg-mass and down into the shadow with delicate countershading. To explain this fact one may apparently appeal only to natural selection, or to sex-limited inheritance of the effect of exposure through many generations.

Other points of interest concern the striking color changes of thirteen species of fishes, which depend upon the color of the objects surrounding the animals. Further study will extend the list. These statements are based upon many records, of which a few were made under laboratory conditions. The greater number by far refer, however, to unconfined specimens studied from a boat, or from the bottom with diving equipment. The various phases of those which will gather about food provided for them may be induced at will by leading the creatures from place to place whose dominant colors differ. Changes of others obey the same laws and may be forecast with precision though they are not demonstrable with the same ease in uncontrolled individuals. Pictures taken with a submarine camera in ten feet of water record some of the observed changes, and show that their general effect is to reduce the conspicuousness of the animals that display them.

The distribution of colors among the various species examined has been investigated in a third phase of the research, and evident correlation of color with habit has been demonstrated. The results obtained may be expressed in brief as follows:

Those fishes in whose coloration red normally predominates are nocturnal, and, in proportion to their numbers, are rarely seen by day.

Gray appears with very different frequency among reef-ranging species and those whose diurnal activity is centered among the coral heads. The ratio of its occurrence in the two cases is roughly commensurate with that of its appearance in the environment of the contrasted groups. Among thirty-one reef-rangers, to state the facts in detail, fourteen show evident adaptive gray color phases or have permanent gray markings, while the same is true of only three of twenty-one species which remain near the coral heads by day. This is equivalent to saying that according to present information gray markings or color phases are about three times as common among reef-ranging fishes as they are among those which live close to the coral heads.

Brown appears so frequently in combination with gray in the patterns of fishes which adapt their coloration almost instantaneously to gray or brown bottoms, whenever the character of their surroundings changes, that in default of special evidence to that effect no functional conspicuousness may be imputed to either color alone, or in combination with the other. The same seems to be true of yellow.

Among the Tortugas fishes the lighter blues at least are correlated with the habit of swimming habitually well above the bottom in water of moderate depth. These tints are peculiarly inconspicuous in the eyes of an observer at a lower level, and photographs of fishes banded with other colors show that the effect of the blue is to blot out its possessor's contour under that condition, since at a distance of a few feet the blue-gray elements in patterns are indistinguishable from the color of the watery background.

Finally, two-thirds of the species seined upon the green grass-flats along shore, and with any show of reason considered typical members of the bionomic association inhabiting such places, are wholly or largely of a green color, or regularly show a green color phase amid green surroundings. If the forms that swim at a high level in open water be excluded, no other such aggregation of green fishes as may be secured on the grass flats may be named from the entire fish fauna of the region, though this includes more than two hundred species.

It seems significant that the suggestion from the observations so far recorded is uniform. The obliterative effect of countershading is demonstrated by Thayer's experiments. That adaptive color changes are very common and minister to the same end, although they occur among bright colored species, is a fair inference from my own experience. The colors of the fishes, also, are correlated with their habits in such

a way that, upon the average, their conspicuousness would apparently be increased if their pigments were very different from those they display.

Additional research demonstrates that in so far as this class of animals is concerned there is no ground for the belief that bright color is correlated in any way with armament or distastefulness. If a list of species possessing organs capable of inflicting painful bodily injury be compiled, their colors and ability to change them are found to differ in no essential respect from those of any other group of the same size selected at random. That no unpalatability is correlated with gaudy coloration is proved by the fact that forms unsurpassed in brilliancy constitute an important part of the food, and may be recovered regularly from the stomachs of snappers, which are among the commonest of the predaceous fishes of the Tortugas. Hence, in view of all the evidence, it seems improbable, to say the least, that the bright colors of some fishes differ in function from the dull hues of their more modest congeners. But since the most highly colored of these creatures vie with birds and butterflies in vividness of coloration, it becomes necessary to revise all hypotheses which postulate conspicuousness.

It is interesting to find that mimicry among insects may be explained much more consistently than is otherwise possible upon the assumption that even the colors of the most gaudy tend to reduce their visibility. Every authenticated fact adduced by the supporters of the mimicry hypotheses may be accounted for, and most, if not all of the criticism levelled against them may be met, if the matter be set forth as follows:

Mimicry has arisen through bionomic pressure applied first by indiscriminate feeders, which have forced upon their accustomed prey color combinations which most effectually conceal it in its normal environment. In addition, by chance, in a few of many thousands of cases in which colors appropriate to the surroundings and habits of their possessors have been evolved, patterns have appeared, sufficiently like one another to deceive enemies that exercise discrimination in their choice of food. From this point onward the evolution of resemblance has proceeded according to accepted formulae, without conspicuousness being involved in the process.

We may assume that the *Pieridae* and *Heliconidae*, for example, are usually distinctly different in habit, and that the coloration of typical members of each family is a combination of hues well suited upon the average to render them inconspicuous in such places as they frequent. If this be so, the initial step toward mimicry might be any one of many

variations in nutrition or reproduction which would lead representatives of the first family to live after the manner of the second. Reason has already been given for supposing that convergence in color would accompany convergence in habit.

Whatever may eventually prove to be the case with the problem of mimetic resemblance, the observations presented in this abstract embody a great mass of fact whose theoretical significance is obvious. It undermines many speculative explanations of animal coloration in terms of natural selection, but, being itself consistent with the Darwinian hypothesis, it replaces them by something which may not be lightly dismissed from consideration. It emphasizes the common occurrence among animals of attributes of apparent advantage to them, and forces the issue between natural selection and the inheritance of acquired characters as the immediate cause of adaptation.

NOTICES OF BIOGRAPHICAL MEMOIRS

The following biographical memoirs have been published by the Academy since the last notices of such memoirs appeared in the November, 1915, number of the PROCEEDINGS.

GEORGE WILLIAM HILL (1838–1914). By ERNEST W. BROWN. *Biographical Memoirs of the National Academy*, **8**, pp. 275–309.

This Memoir discusses the life-work of George W. Hill along the following outline: Boyhood, First papers; Influence of Delaunay and Hansen, Comet of 1858, Elements of Venus, the Years 1872–1875; the Great Decade 1875–1885, Hill's Mental Development, Astronomy before Hill, the Two Great Memoirs of 1877, Influence of Euler, the Periodic Orbit, Stability, Infinite Determinants, Relation to J. C. Adams' Work, Theories of Jupiter and Saturn, Estimate by F. R. Moulton; Residence in Washington, Application of the Methods of Delaunay, Hansen, de Pontécoulant, and Gauss; Concluding years, Hill's Characteristics, Estimates by Poincaré, R. S. Woodward, A. S. Flint, H. B. Hedrick, and H. Jacoby; Hill's Scientific Honors; Bibliography.

THEODORE NICHOLAS GILL (1837–1914.) By WILIAM HEALEY DALL. *Biographical Memoirs of the National Academy*, **8**, pp. 313–343.

This Memoir recounts the life-work of Theodore N. Gill: Boyhood, Report on the Fishes of New York, Trips to the Antilles and Newfoundland; Connections with the Smithsonian Institution, the Library of Congress, and the U. S. Fish Commission; Editor of the *Osprey* Work on Mollusca; Estimates by the Commissioner of Fisheries, by the Director of the National Museum; Associations with George Washington University; Personal Characteristics; Bibliography.